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Calcium in plant peroxisomes. What for?

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ABSTRACT

Peroxisome organelles have a versatile metabolism whose enzymatic content can be modulated by physiological and environment-dependent cellular conditions. They are characterized by a highly active nitro-oxidative metabolism and basic elements (H_2O_2 and nitric oxide (NO)) with signaling properties. However, new elements have increased our understanding of the connections between peroxisomes and other cellular compartments. Furthermore, the presence of calcium (Ca^{2+}) intensifies communication between different signaling molecules and the relationship of Ca^{2+} itself with NO and H_2O_2.

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At the biochemical level, peroxisomes have been defined as subcellular compartments containing catalase and H_2O_2-producing flavin oxidases as basic enzymatic constituents surrounded by a single membrane.[1-3] However, behind the apparently simple morphology of plant peroxisomes, there is a complex biochemical machinery characterized by flexibility, which endows them with a great capacity to modulate their metabolism according to physiological and environment-dependent cellular conditions.[4,5]

Peroxisomes are widely recognized to be involved in classic pathways such as photorespiration, the glyoxylate cycle and fatty acid β-oxidation. However, over the last twenty years, new enzymatic and non-enzymatic components in these organelles, such as hormone biosynthesis and polyamine catabolism, have been reported, which has increased our understanding of their complex metabolism.[2,5-7] Peroxisomes have been found to be a source of nitric oxide (NO) and other NO-derived molecules which extends our knowledge of the highly active oxidative metabolism to a close family of molecules called reactive nitrogen species (RNS) which are also involved in physiological and stress processes.[5]

Calcium (Ca^{2+}), which is a mineral nutrient element essential for plant growth and development, is involved in numerous processes such as root development, cell division, stomatal movement, as well as pathogen and abiotic stress responses.[8] Ca^{2+}, whose cellular fluctuations can modulate the activity of many pathways, is considered to be a universal intracellular second messenger.[9] Biochemical sensors, which decode Ca^{2+} signals into specific physiological responses, include calmodulin (CaM), calmodulin-like proteins, Ca^{2+}-dependent protein kinases (CDPKs) and calcineurin B-like (CBL) proteins.[10,11] At the subcellular level, the presence and importance of Ca^{2+} in the different subcellular compartments, including the cytosol, nucleus, chloroplasts and mitochondria, have been demonstrated and analyzed extensively.[12-16] Surprisingly, the presence and potential significance of Ca^{2+} in plant peroxisomes is less well known, and only a few studies have reported its occurrence in these organelles.[17,18] There is also evidence that plant peroxisomes house some of the biochemical sensors mentioned above such as calcium-dependent protein kinase 1 (AtCPK1) involved in pathogen resistance,[19] the CaM-like protein (AtCML3), which mediates the dimerization of peroxisomal processing protease AtDEG15,[20] and Ca-dependent protein kinase 2 (PiCDPK2) involved in regulating pollen tube growth in *Petunia inflate*.[21]

Based on information currently available, Fig. 1 illustrates a working model which shows the functional involvement of Ca^{2+} in the metabolism of plant peroxisomes and especially in NO biosynthesis. Two principal targeting signals, which direct proteins into the peroxisomal matrix, have so far been described: peroxisomal targeting signal type 1 (PTS1) at the C terminus and peroxisomal targeting signal type 2 (PTS2) at the N terminus of the protein. By using Arabidopsis mutants expressing chimeric fluorescent proteins with either PTS1 or PTS2, it has been possible to demonstrate that Ca^{2+} and CaM are necessary for the import of peroxisomal matrix proteins with both types of PTS.[22,23] These include the protein responsible for NO generation from L-arginine inside peroxisomes which appear to contain PTS2.[22] Additionally, NO synthase (NOS)-like activity present in these organelles also requires the presence of Ca^{2+} and CaM.[24] On the other hand, NO can mediate post-translational modifications, such as nitration and *S*-nitrosation, which regulate the protein functions of affected targets such as catalase and hydroxypyruvate reductase. In certain circumstances, NO can go out to the cytosol and participate in either signaling or responses to environmental stresses caused by salinity, cadmium and lead.[25-27] Ca^{2+} can thus modulate the generation of peroxisomal NO and consequently initiate a cascade of signals through NO-derived post-translational modifications. Catalase, which is

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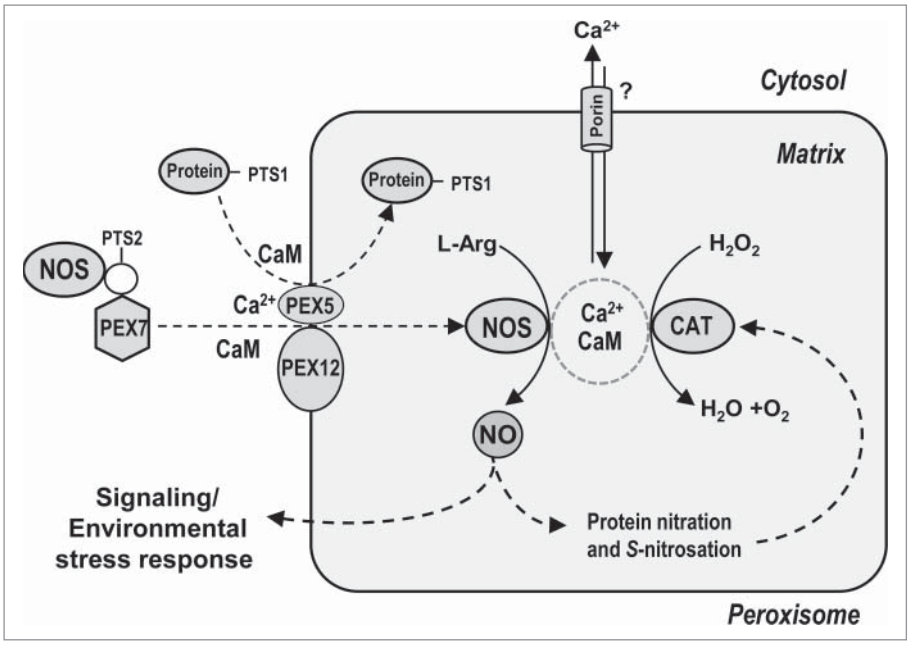

Figure 1. Simple model of the functional implication of calcium (Ca^{2+}) and calmodulin (CaM) in the metabolism of plant peroxisomes. Ca^{2+} could move in peroxisomes through a porin ion channel located in the peroxisomal membrane. Ca^{2+} and CaM modulate some of the peroxisomal enzyme such as catalase as well of the L-Arg dependent NO synthase-like activity which regulates the H_2O_2 and NO content, respectively. Import of peroxisomal matrix proteins requires the participation of different peroxins (PEX) such as the PEX12 located in the membrane and both PEX5 and PEX7 PTS receptors located in the cytosol. In this process Ca^{2+} and CaM are also necessary. NO can mediate post-translational modifications (nitration and *S*-nitrosation) of peroxisomal proteins such as catalase or it can function as signal molecule outside of the peroxisomes or in a process of environmental response.

the main antioxidant peroxisomal enzyme, is also regulated not only by Ca^{2+} and CaM[28] levels but also by NO-derived molecules; thus, H_2O_2 content is indirectly regulated by the level of NO, with a clear connection being observed between ROS and RNS metabolisms in these organelles.

However, these data are merely the first step in an analysis of the importance of calcium in plant peroxisomes.[29] The following issues need to be resolved in future research: how Ca^{2+} and CaM move through the peroxisomal membrane; identification of new potential protein targets in the peroxisomal import system and in the regulatable peroxisomal metabolism.

Abbreviations

AtCPK1	calcium-dependent protein kinase 1
GSH	reduced glutathione
GSNO	*S*-nitrosoglutathione
NO	nitric oxide
NOS	nitric oxide synthase
PEX	peroxin
PiSCP1	*Petunia inflata* small CDPK-interacting protein 1
PTS1	peroxisomal targeting signal type 1
PTS2	peroxisomal targeting signal type 2
RNS	reactive nitrogen species

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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References

1. Hayashi M, Nishimura M. Entering a new era of research on plant peroxisomes. Curr Opin Plant Biol. 2003;6:577–82. doi:10.1016/j.pbi.2003.09.012.
2. Hu J, Baker A, Bartel B, Linka N, Mullen RT, Reumann S, Zolman BK. Plant peroxisomes: biogenesis and function. Plant Cell. 2012;24:2279–303. doi:10.1105/tpc.112.096586.
3. Corpas FJ. What is the role of hydrogen peroxide in plant peroxisomes? Plant Biol (Stuttg). 2015;17:1099–103. doi:10.1111/plb.12376.
4. Hayashi M, Toriyama K, Kondo M, Kato A, Mano S, De Bellis L, Hayashi-Ishimaru Y, Yamaguchi K, Hayashi H, Nishimura M. Functional transformation of plant peroxisomes. Cell Biochem Biophys. 2000;32:295–304. doi:10.1385/CBB:32:1-3:295.
5. Corpas FJ, Barroso JB, Palma JM, Rodríguez-Ruiz M. Plant peroxisomes: A nitro-oxidative cocktail. Redox Biol. 2017;11:535–42. doi:10.1016/j.redox.2016.12.033.
6. Palma JM, Corpas FJ, del Río LA. Proteome of plant peroxisomes: new perspectives on the role of these organelles in cell biology. Proteomics. 2009;9:2301–12. doi:10.1002/pmic.200700732.
7. Reumann S, Bartel B. Plant peroxisomes: recent discoveries in functional complexity, organelle homeostasis, and morphological dynamics. Curr Opin Plant Biol. 2016;34:17–26. doi:10.1016/j.pbi.2016.07.008.
8. Hepler PK. Calcium: a central regulator of plant growth and development. Plant Cell. 2005;17:2142–55. doi:10.1105/tpc.105.032508.
9. Choi WG, Hilleary R, Swanson SJ, Kim SH, Gilroy S. Rapid, long-distance electrical and calcium signaling in plants. Annu Rev Plant Biol. 2016;67:287–307. doi:10.1146/annurev-arplant-043015-112130.
10. Luan S, Kudla J, Rodriguez-Concepcion M, Yalovsky S, Gruissem W. Calmodulins and calcineurin B-like proteins: calcium sensors for

specific signal response coupling in plants. Plant Cell. 2002;14(Suppl): S389–400. doi:10.1105/tpc.001115.
11. Tuteja N, Mahajan S. Calcium signaling network in plants: an overview. Plant Signal Behav. 2007;2:79–85. doi:10.4161/psb.2.2.4176.
12. Charpentier M, Oldroyd GE. Nuclear calcium signaling in plants. Plant Physiol. 2013;163:496–503. doi:10.1104/pp.113.220863.
13. Nomura H, Shiina T. Calcium signaling in plant endosymbiotic organelles: mechanism and role in physiology. Mol Plant. 2014; 7:1094–104. doi:10.1093/mp/ssu020.
14. Hochmal AK, Schulze S, Trompelt K, Hippler M. Calcium-dependent regulation of photosynthesis. Biochim Biophys Acta. 2015;1847:993–1003. doi:10.1016/j.bbabio.2015.02.010.
15. Edel KH, Marchadier E, Brownlee C, Kudla J, Hetherington AM. The evolution of calcium-based signalling in plants. Curr Biol. 2017;27: R667–79. doi:10.1016/j.cub.2017.05.020.
16. Kudla J, Becker D, Grill E, Hedrich R, Hippler M, Kummer U, Parniske M, Romeis T, Schumacher K. Advances and current challenges in calcium signaling. New Phytol. 2018. doi:10.1111/nph.14966.
17. Costa A, Drago I, Behera S, Zottini M, Pizzo P, Schroeder JI, Pozzan T, Lo Schiavo F. H_2O_2 in plant peroxisomes: an in vivo analysis uncovers a Ca^{2+}-dependent scavenging system. Plant J. 2010;62:760–72. doi:10.1111/j.1365-313X.2010.04190.x.
18. Corpas FJ, Barroso JB. Calmodulin antagonist affects peroxisomal functionality by disrupting both peroxisomal Ca^{2+} and protein import. J Cell Sci. 2018;131(2). doi:10.1242/jcs.201467.
19. Coca M, San Segundo B. AtCPK1 calcium-dependent protein kinase mediates pathogen resistance in Arabidopsis. Plant J. 2010;63:526–40. doi:10.1111/j.1365-313X.2010.04255.x.
20. Dolze E, Chigri F, Höwing T, Hierl G, Isono E, Vothknecht UC, Gietl C. Calmodulin-like protein AtCML3 mediates dimerization of peroxisomal processing protease AtDEG15 and contributes to normal peroxisome metabolism. Plant Mol Biol. 2013;83:607–24. doi:10.1007/s11103-013-0112-6.
21. Guo F, Yoon GM, McCubbin AG. PiSCP1 and PiCDPK2 localize to peroxisomes and are involved in pollen tube growth in *Petunia inflata*. Plants (Basel). 2013;2:72–86. doi:10.3390/plants2010072.
22. Corpas FJ, Barroso JB. Peroxisomal plant nitric oxide synthase (NOS) protein is imported by peroxisomal targeting signal type 2 (PTS2) in a process that depends on the cytosolic receptor PEX7 and calmodulin. FEBS Lett. 2014;588:2049–54. doi:10.1016/j.febslet.2014.04.034.
23. Corpas FJ, Barroso JB. Peroxisomal plant metabolism - an update on nitric oxide, Ca^{2+} and the NADPH recycling network. J Cell Sci. 2018;131(2). doi:10.1242/jcs.202978.
24. Corpas FJ, Barroso JB, Carreras A, Quirós M, León AM, Romero-Puertas MC, Esteban FJ, Valderrama R, Palma JM, Sandalio LM, et al. Cellular and subcellular localization of endogenous nitric oxide in young and senescent pea plants. Plant Physiol. 2004;136:2722–33. doi:10.1104/pp.104.042812.
25. Corpas FJ, Hayashi M, Mano S, Nishimura M, Barroso JB. Peroxisomes are required for *in vivo* nitric oxide accumulation in the cytosol following salinity stress of Arabidopsis plants. Plant Physiol. 2009;151:2083–94. doi:10.1104/pp.109.146100.
26. Corpas FJ, Barroso JB. Peroxynitrite ($ONOO^-$) is endogenously produced in Arabidopsis peroxisomes and is overproduced under cadmium stress. Ann Bot. 2014;113:87–96. doi:10.1093/aob/mct260.
27. Corpas FJ, Barroso JB. Lead-induced stress, which triggers the production of nitric oxide (NO) and superoxide anion ($O_2^{\cdot-}$) in Arabidopsis peroxisomes, affects catalase activity. Nitric Oxide. 2017;68:103–10. doi:10.1016/j.niox.2016.12.010.
28. Yang T, Poovaiah BW. Hydrogen peroxide homeostasis: activation of plant catalase by calcium/calmodulin. Proc Natl Acad Sci USA. 2002;99:4097–102. doi:10.1073/pnas.052564899.
29. Stael S, Wurzinger B, Mair A, Mehlmer N, Vothknecht UC, Teige M. Plant organellar calcium signalling: an emerging field. J Exp Bot. 2012;63:1525–42. doi:10.1093/jxb/err394.